Ungulate control of grassland production: grazing intensity and ungulate species composition in Yellowstone Park

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Abstract.   Knowledge of the envelope of grazing conditions within which grassland plant and soil processes are sustainable is important for the ecologically sound management of grazed grassland. Here we examined how a recent shift from elk to bison dominance of the northern ungulate community in Yellowstone National Park (YNP), and an associated increase in the duration that grassland was grazed, affected grazing intensity and aboveground net primary production (ANPP). Mean grazing intensity (GI, percentage ANPP removed) and stimulation (grazed ANPP minus ungrazed [exclosed] ANPP) were compared among three studies, two when elk (1988–1989, 1999–2001) and one when bison (2012–2014) dominated the northern YNP ungulate community. We also manipulated GI with small exclosures established for different lengths of time after the start of the growing season to directly determine the effect of the combination of grazing duration (GD) and GI on stimulation at a dry grassland and a mesic grassland. GI was greater under a bison-dominant grazing regime (49%) compared with that measured during the two earlier periods when elk were the dominant ungulate species (31%, 13%). Plotting stimulation on GI for sites sampled across all three studies revealed a unimodal relationship, with peak stimulation of 34% occurring at a GI of 40%. Manipulating GI indicated that the greater GI and longer GD of grazing under a bison-dominant regime reduced stimulation at a mesic grassland and negated it completely at a dry grassland. These findings revealed that a shift in the grazing ungulate community composition and an associated change in the migratory behavior of the dominant species impacted YNP grassland processes. Results also showed that grassland ANPP was resilient to the relatively high rates of prolonged grazing by the bison-dominant community and did not reduce ANPP below paired, ungrazed conditions. However, YNP grassland should be continued to be monitored if such high rates of herbivory continue.

Key words: bison; elk; grassland; herbivory; ungulate; Yellowstone National Park.

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INTRODUCTION

Studies in different types of grasslands have revealed that the response of grassland production to grazing differs qualitatively depending on several contingent factors. Grazers tend to stimulate plant production when soil resources (i.e., nutrient, moisture) are abundant, grazing is light to intermediate, and animals and plants have long coevolutionary histories. In contrast, large herbivores have neutral to negative effects on grassland production when resources are low, grazing intensities are high, and there is a short shared coevolutionary history between grazers and plants (Milchunas et al. 1988, Milchunas and Lauenroth 1993, De Mazancourt et al. 1998, Porensky et al. 2013). However, for most grasslands supporting herds of grazing herbivores, there is no quantitative information about the envelope of the combination of site and grazing

conditions that ecosystem processes and services are sustainable. Such information would be helpful to guide long-term ecological sound management of grazed ecosystems.

In this study, we examined how a recent shift from elk (*Cervus elaphus*) to bison (*Bison bison*) dominance of the northern range ungulate community in Yellowstone National Park (YNP) and an associated increase in the duration of spring–summer–fall grazing have influenced plant production. The northern Yellowstone elk population spends winter along the Yellowstone River drainage in the northern portion of YNP and nearby areas of Montana. Counts of northern elk increased exponentially after the cessation of elk culling that was imposed to reduce their abundance during the 1930s through the 1960s (Houston 1982; Fig. 1). The northern elk numbers peaked in the late 1980s and remained relatively high until the mid-1990s, after which wolf predation, reinforced by a larger grizzly bear population, continued human harvests, and an extreme regional drought that ended in 2007 led to a precipitous decline and maintenance of a much smaller northern elk population (Eberhardt et al. 2007, Barber-Meyer et al. 2008, van Manen et al. 2016; Fig. 1). Bison numbers remained low on the northern Yellowstone range through the 1980s and 1990s (mean 700), but began to increase in 2004 and reached a peak of 3421 animals in 2014. One reason for the increase was a redistribution of a large number of bison from the central portion of the park to northern Yellowstone during the past decade (White and Wallen 2012). Bison and elk compete for forage in YNP (Houston 1982, Coughenour 2005, Plumb et al. 2009). Consequently, northern herd bison also may have increased because of the substantial decrease in elk numbers and an increase in available forage. Pronghorn (*Antilocarpa americana*), which also graze YNP grassland, have remained a relatively minor component of the YNP ungulate community (Fig. 1).

We were interested in how the shift in the dominant ungulate species and the associated change in grazing patterns have influenced aboveground production (ANPP) in northern range grasslands of YNP. Previously (Frank and McNaughton 1992), it was shown that elk preferentially fed on young, nutritious vegetation
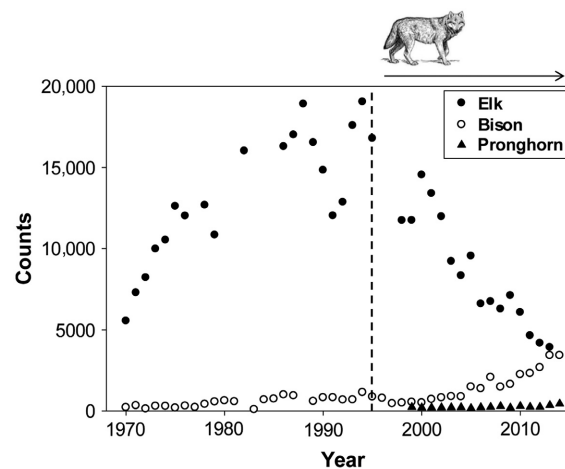

Fig. 1. Counts of bison, elk, and pronghorn, the three major Yellowstone National Park (YNP) grazing ungulate species, in and near northern Yellowstone during 1970 to 2014. Elk and pronghorn were counted during winters and bison during summers. The dashed line indicates when wolves were reintroduced in YNP. Counts were conducted by the Northern Yellowstone Cooperative Wildlife Working Group, which consists of Montana Fish, Wildlife and Parks, National Park Service, U.S. Forest Service, and U.S. Geological Survey.

sweeping up the elevation gradient through the spring and summer. As a consequence, grassland communities were primarily grazed for the first 1–2 months after snowmelt when elk dominated the northern range ungulate community (Frank and McNaughton 1992). Grazing was found to facilitate ANPP under those conditions, increasing production by 43% and 22% during studies conducted in 1988–1989 and 1999–2001, respectively (Frank et al. 1998, 2002), with smaller facilitating effects during years of drought (Frank 2007). In recent years, large numbers of bison have remained in the lower Lamar River Valley grazing grassland throughout the snow-free season that previously, when elk dominated the community and there were fewer bison, was grazed only during the first 1 or 2 months during the growing season. The objectives of this study were to compare grazing intensities and the response of grassland ANPP among the three studies. We were particularly interested in how the extended duration of grazing by dense bison influenced the previously observed (Frank and

McNaughton 1993, Frank et al. 2002, Frank 2007) positive feedback that YNP ungulates had on ANPP.

MATERIALS AND METHODS

Study area

Yellowstone National Park is an 8995-km^2 mountainous preserve in the central Rocky Mountains of North America. The Park's climate includes long cold winters and dry summers with mean annual temperature decreasing and precipitation increasing with elevation. For example, 30-year (1984–2014) mean annual temperature and precipitation at Tower Falls, located on low-elevation (2012 m) northern winter range, were 2.4°C and 40.6 cm and at Lake Ranger Station, located on high-elevation summer range (2357 m), were −1.5°C and 55.5 cm (Fig. 2). Soils throughout the Park have developed primarily on mineral material deposited during the Pleistocene (Keefer 1987).

Yellowstone National Park supports eight species of ungulates. This study focuses on elk, bison, and pronghorn because they were the principal ungulates feeding at our study sites. Other ungulates that occur in the Park include bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*) that primarily graze cliffs, ridgetops, and steep high-elevation slopes, and mule deer (*Odocoileous hemionus*), moose (*Alces alces*), and white-tailed deer (*Odocoileous virginianus*) that are rarely observed grazing grassland.

Study periods

This study examines factors that govern the response of ANPP to ungulate grazing during
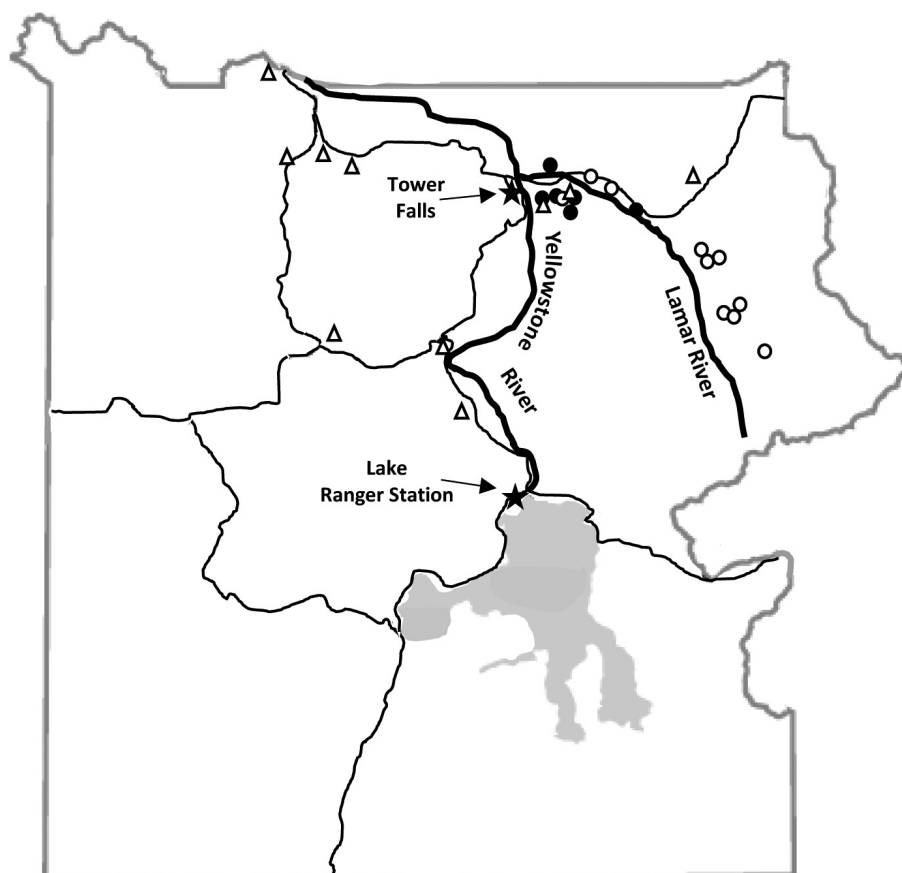

Fig. 2. Map of Yellowstone National Park with the locations of the study sites during the 1988–1989 (open circles), 1999–2001 (triangles), and 2012–2014 (closed circles) studies and weather stations (stars) referenced in the text.

three time periods when the size and composition of the YNP grazer community were different. During the first study (1988–1989), elk were the predominant ungulate herbivore. The maximum elk count in northern YNP and nearby areas of Montana was 18,913 during that period (Fig. 1). During the second study (1999–2001), elk remained the dominant ungulate grazer, but the high count decreased to 14,538. Elk-dominated herbivory was found to stimulate YNP grassland production during both of those study periods (Frank and McNaughton 1993, Frank et al. 2002). During the third study (2012–2014), high counts of elk were 20% (4174) and bison were 478% (3420) of the maximum counts in 1988–1989. The peak pronghorn count was 351 during 2012–2014. Because of differences in numbers and body mass among species, ungulate biomass was dominated by elk during the first two study periods and bison during the last (Fig. 3). Total ungulate biomass declined during the three studies from an estimated 5.0 million kg in 1988–1989 to 3.7 million kg in 1999–2001 to 2.3 million kg in 2012–2014. Because consumption rate per unit mass is inversely related to animal body mass (Peters 1986), total ungulate consumption by the entirety of the ungulate community likely declined across the northern range more steeply than did the decline in herbivore biomass.

During the two earlier studies (1988–1989, 1999–2001), elk, bison, and, to a lesser extent,
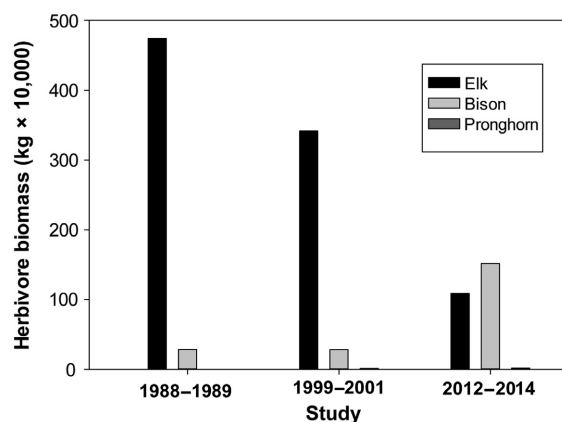

Fig. 3. Elk, bison, and pronghorn biomass during the three study periods. Values were derived from population counts, herd adult male: female and adult: young ratios, and respective biomass estimates from the literature (Houston 1982, O'Gara 1970).

pronghorn left low-elevation winter range in the lower Yellowstone and Lamar River drainages (Fig. 2) in the spring (April–May) and migrated upslope to graze high-elevation sites during June through September (Frank and McNaughton 1992, Frank et al. 1998). The 2012–2014 study was conducted during a period when bison replaced elk as the dominant grazing ungulate species and large numbers of bison grazed low-elevation range in the lower Lamar River drainage through the growing season (April to September) that formerly, during the previous two studies, was little grazed after most animals migrated to high-elevation range in the spring. The objective of the former two studies was to examine grazing dynamics in grasslands that varied widely in seasonal use and elevation. Grasslands included in the 2012–2014 study when bison dominated were spatially constrained to an area in the lower Lamar River drainage that supported large numbers of bison through the growing season (Fig. 2; Geremia et al. 2014). The objective of the third study was to measure consumption rates and the response of grassland ANPP to the sustained growing season-long bison grazing regime.

Measurements

During each of the three studies, we measured ANPP, ungulate consumption, and the response of grassland production to grazing (i.e., stimulation). Consumption and ANPP (accounting for plant biomass removed by grazers) in grazed grassland were determined with replicated moveable exclosures randomly located at each grassland study site (e.g., Frank and McNaughton 1992, Frank et al. 2002). Moveable exclosures were 1.5×1.5 m in area, established within 2 weeks after snow melted, and randomly relocated monthly through the growing season at each site. A monthly rate of consumption was calculated as a significant difference ($\alpha = 0.05$) in biomass between aboveground plant biomass inside vs. outside moveable exclosures (Frank and McNaughton 1992). Aboveground production was determined as a significant increment in standing biomass inside moveable exclosures. Annual ANPP and growing season consumption were derived by summing values across the growing season.

Aboveground net primary production in ungrazed grassland was determined in permanent exclosures ($n = 1$–3 per site; Frank and

McNaughton 1992, 1993, Frank et al. 2002, Frank 2007). Permanent exclosures were established at subgroups of grassland sites during the 1988–1989 (three of 10) and 2012–2014 (two of six) studies and at all 10 sites during the 1999–2001 study. Exclosures were established 1 year prior to each of the three studies and were either 10 × 10 m or 15 × 15 m, depending on the size and configuration of the grassland sampled. Aboveground production in ungrazed grassland at each site was determined by statistically significant increments of aboveground biomass inside permanent exclosures. Aboveground biomass was determined in 5–10 0.5-m^2 quadrats in each permanent exclosure. ANPP of ungrazed grassland was calculated similar to grazed grassland. Plant standing biomass, including graminoid vs. dicot biomass, in grazed grassland and in temporary and permanent exclosures was measured with the canopy intercept method (Frank and McNaughton 1990, 1992).

Stimulation at a grassland was derived by subtracting ungrazed from grazed ANPP. We examined factors controlling stimulation in two ways. First, we pooled data from the three studies to model stimulation as a function of grazing intensity and site condition, which was indexed with ANPP of ungrazed grassland. Second, we experimentally manipulated ungulate grazing at a dry grassland and a mesic grassland in 2012 and 2014 to directly test how grazing intensity and site condition influenced stimulation. We varied grazing by randomly locating replicated ($n = 3$), 1.5 × 1.5 m exclosures that were fixed in place after animals grazed each grassland for 1–3 months after snowmelt. This resulted in three grazing intensity/duration treatments at the dry and two treatments at the mesic grassland, in addition to the no grazing (permanently fenced) and the season-long grazing treatment (measured with moveable exclosures) at both sites. ANPP for the ungrazed period of the season for each of the fixed exclosure groups was determined by summing statistically significant increments of shoot biomass inside exclosures. Because the timing and intensity of grazing (e.g., early-season and light grazing vs. season-long and heavy grazing) covaried, the manipulation examined the combined effects of timing and intensity of grazing on stimulation.

In addition to testing the effects of GI and site condition on stimulation, we examined two factors that may have influenced stimulation differentially among the three studies. First, stimulation may have differed among the three studies because of differences in available moisture during the study periods or because of latent effects from climatic conditions that occurred in years preceding the studies. We examined differences in moisture conditions among study periods by comparing April–September (growing season, GS) and December–September ("water year," WY, the precipitation available to plants as moisture stored as snow during the preceding winter and rainfall during the growing season) from weather records at the Tower Falls weather station among the three study periods. In addition, we determined whether there was a systematic shift in moisture conditions at Tower Falls during the period 1988–2014 by testing for a significant slope when plotting GS and WS on year. Second, different grazing preferences by elk and bison may have led to different grassland species compositions that influenced how grasslands responded to grazing. To explore the potential effect of grazer feeding preference on grassland composition, we examined whether herbivory led to differences in the relative contribution of graminoid biomass to total plant biomass among the studies. We calculated this herbivore effect by subtracting the percentage graminoid biomass in ungrazed (permanently fenced) from grazed grassland the month that ungrazed biomass peaked.

Statistical analyses

We examined the relationship between consumption and grassland ANPP, a strong covariate with grazing, for the 2012–2014 study with least square regression and compared it to similar analyses previously published for the 1988–1989 (Frank and McNaughton 1992) and 1999–2001 studies (Frank 2008a). Least square regression also was used to examine the relationships of GS and WY on year. We pooled data from all three studies to model stimulation (as percentage of ungrazed NAP) as a function of grazing intensity (GI, as percentage of ANPP) and site condition. Akaike's information criterion for small sample size (AIC$_c$) was used for model selection (Burnham and Anderson 2002). GI and percentage stimulation were arcsine-transformed

to normalize data. All statistical tests were performed in R version 2.14.1 (R Development Core Team 2014). Consumption, stimulation, GS, and WY were modeled using the *lm* function.

RESULTS

Grazing intensity

Aboveground net primary production ranged widely among grasslands included in each of the three studies (Fig. 4), primarily reflecting the topo-edaphic gradients (hilltop to slope-bottom) that were sampled in the studies (Frank 2008*a*). Ungulate consumption rates increased linearly with ANPP during the 1988–1989 study when elk were dominant (Frank and McNaughton 1992) and during the high-bison (2012–2014) study. During the 1999–2001 study, when elk still dominated but were lower in number, consumption increased linearly from low to intermediately productive grassland and then declined at the more productive sites (ANPP > 200 g/m^2; Frank 2008*a*).

The slope of the consumption–ANPP function during the high-bison study period was greater than those for the 1988–1989 period and the positive linear phase for the 1999–2001 period
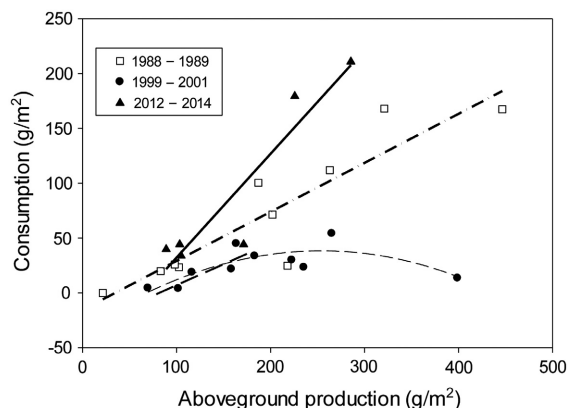

Fig. 4. The relationship of ungulate consumption (Cons) on net aboveground production (ANPP) in grasslands of Yellowstone National Park for the three studies. Regression lines are as follows: 1988–1989: Cons = 0.44(ANPP)–15.4, $r^2 = 0.82$, $P < 0.001$ (Frank and McNaughton 1992); 1999–2001 (quadratic): Cons = 0.56(ANPP)–0.001(ANPP^2)–33.2, $r^2 = 0.62$, $P < 0.033$ (Frank 2008*a*); 1999–2001 (linear phase): Cons = 0.32(ANPP)–21.1, $r^2 = 0.74$, $P = 0.028$; 2012–2014: Cons = 0.95(ANPP)–62.3; $r^2 = 0.87$, $P < 0.001$.

when elk dominated the ungulate community ($P = 0.029$). Mean GI (calculated among years during each study) ranged from 26% to 74% among grasslands when bison dominated and was greater (49% $\pm$ 5%; mean $\pm$ SE) than when elk dominated during 1988–1989 (31% $\pm$ 8%) and 1999–2001 (13% $\pm$ 2.4%; $P = 0.001$).

Effect of grazing on ANPP

Stimulation was best described as a unimodal function of GI (Fig. 5). Both GI and GI^2 were significant terms in the polynomial relationship ($P = 0.02$ and 0.05, respectively), and AIC$_c$ of the second-order polynomial relationship was less (132.9) than that of the full model that included site condition (136.1), indexed by ungrazed ANPP. Back transforming the arcsine values in Fig. 5 revealed that stimulation peaked at 34% at a grazing intensity of 40%.

We directly tested how the combination of grazing duration and GI affected stimulation at two grasslands. Grazing intensity monotonically declined with the number of months plots were fenced at both the dry and mesic grasslands during the grazing manipulation experiment. Stimulation patterns varied markedly between the two grasslands (Fig. 6). Peak stimulation at the dry grassland was lower and occurred at a much lighter grazing intensity compared with the mesic grassland.

April–September (GS) and December–September (WY) precipitation tended to be greater during the high-bison study compared with the earlier two studies (GS: 1988, 17.4 cm; 1989, 23.4 cm; 1999, 26.0 cm; 2000, 23.9 cm; 2001, 19.2 cm; 2012, 27.9 cm; 2013, 21.6 cm; 2014, 31.4 cm; WY: 1988, 25.2 cm; 1989, 36.6 cm; 1999, 37.1 cm; 2000, 37.6 cm; 2001, 24.3 cm; 2012, 31.8 cm; 2013, 31.6 cm; and 2014, 46.4 cm). There was no increasing or decreasing trend in GS ($P = 0.521$) or WY ($P = 0.24$) precipitation during 1986–2014. In addition, study period had no effect on grazer-induced change in the percentage graminoid biomass ($P = 0.651$).

DISCUSSION

Grazing intensity

The linear increase in consumption with ANPP during the 1988–1989 and 2012–2014 studies when elk and bison dominated the ungulate
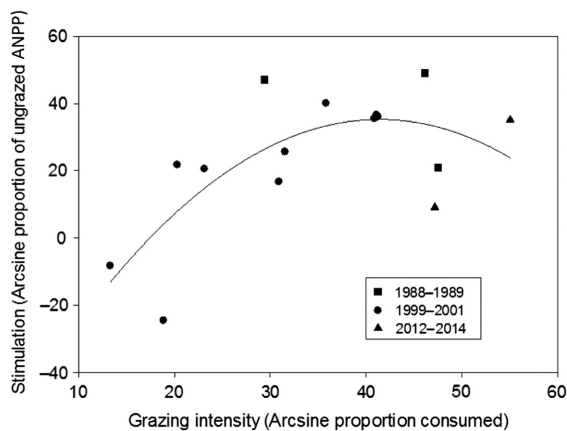
Fig. 5. Relationship between arcsine-transformed percentage aboveground net primary production (ANPP) stimulated by ungulates and arcsine-transformed GI (percentage of ANPP consumed) at Yellowstone National Park grasslands during the three study periods.

community, respectively, reflected site selection by the animals based on forage availability. Mean grazing intensity was greater during 1988–1989 than 1999–2001, because of higher elk numbers (Fig. 3; Frank 2008*a*). The unimodal function in the 1999–2001 study, particularly the decline in consumption among the most productive grasslands, was hypothesized earlier (Frank 2008*a*) as having been a function of elk avoiding high
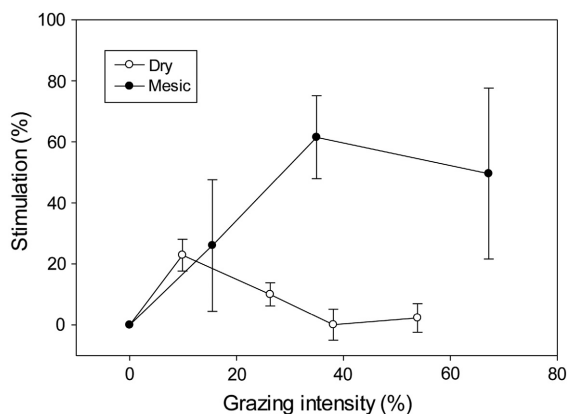

Fig. 6. Mean (±SE) percentage stimulation vs. mean percentage grazing intensity at a mesic grassland and a dry grassland in Yellowstone National Park during 2012–2014.

productive areas at the base of slopes and in swales where visibility to maintain vigilance for wolves was low. Other YNP researchers examining elk feeding behavior have drawn a similar conclusion that elk avoid areas where they are vulnerable to wolf predation (Ripple and Beschta 2004, 2006, Hernandez and Laundré 2005). Elk are the predominant prey (>75%) of wolves, with bison comprising a minor portion (<5%), likely because the latter are larger and use group defenses to thwart attacks (MacNulty et al. 2007, Metz et al. 2012). GI was greatest when bison dominated the ungulate community compared with both of the earlier studies that occurred before and after wolves influenced elk foraging behavior.

The greater slope under a high-bison regime reflected greater preference by bison for highly productive sites, which is consistent with previous observations in YNP (Singer and Norland 1994), southern Utah (Ranglack and du Toit 2015), Kansas (Vinton and Hartnett 1992), and Oklahoma (Shaw and Carter 1990, Coppedge and Shaw 1998). Bison feed preferentially in highly productive grassland because of their large energetic and nutritional demands and long digestive tract that allows them to efficiently extract resources from low-quality bulk forage (Feist 2000).

Ungulate biomass was lower when bison were dominant (Fig. 3), which, combined with an expected lower energy demand per unit biomass than for elk and pronghorn (Peters 1986), should have resulted in lower consumption rates when bison dominated the ungulate community. The explanation for greater herbivory rates during the 2012–2014 study stems from the different migratory feeding behaviors of elk compared with bison. Elk in YNP progressively move upslope during the spring and summer to graze high-quality forage (Frank and McNaughton 1992). This resulted in nearly all animals migrating to higher elevation summer range when elk dominated the YNP ungulate community (Frank and McNaughton 1992). Historically, bison had exhibited a similar seasonal migration to higher summer ranges (Meagher 1973). However, by 1983, a small portion of the northern bison herd began grazing the Lamar Valley through the summer (Taper et al. 2000). Over time, larger numbers of cow–calf groups of bison grazed

grassland areas in the lower Lamar River drainage through the snow-free season and, by 2012, the first year of the latter study, more than 2000 bison grazed the area through the growing season (Blanton et al. 2015). Female bison need to graze highly productive grasslands during the growing season to recover from the effects of winter malnutrition and rear their offspring as rapidly as possible for young to survive the ensuing winter (Treanor et al. 2015). We suspect that a limited total area of highly productive grassland on high-elevation range led to large numbers of bison remaining in the lower Lamar River drainage during the snow-free year. Further studies will be necessary to clarify what the consequences of the increased abundance of bison have been on high-elevation grassland.

Effect of grazing on ANPP

Similar to many temperate grasslands, YNP grassland production is limited by a combination of soil moisture and nitrogen availability (Frank 2007, 2008b). Ungulates in YNP increase soil net N mineralization rates (Frank and Groffman 1998) and leaf nitrogen concentrations (Frank 2008b), which is associated with greater leaf-level carbon assimilation rates (Hamilton and Frank 2001). Grazers also stimulate grassland ANPP in YNP by promoting an arbuscular mycorrhizal fungal (AMF) community that increases plant growth more than the AMF community associated with ungrazed grassland (Frank et al. 2003). Thus, facilitating the availability of soil N for plant uptake and promoting beneficial mycorrhizal partners that can take up that N play important roles in ungulates stimulating grassland ANPP.

Inspection of the unimodal stimulation–GI relationship (Fig. 5) suggests that the bison-dominant community of the 2012–2014 study grazed grassland at intensities greater than herbivory rates that maximized ANPP. This interpretation, however, has two caveats. First, stimulation may have differed among study periods because of climate change, in particular a decline in precipitation that would have inhibited regrowth of grazed plants during the latter study. This, however, was not the case. Moisture tended to be greater during the 2012–2014 study, indicating that a decline in stimulation during the bison-dominant study was not a function of lower moisture. In addition, there was no relationship between GS or WY

precipitation with year (1986–2014), suggesting that moisture conditions did not progressively change during the study period. Second, the grazing ungulate community composition may have had an effect on stimulation because of different forage preferences of the ungulate species. Elk feed more selectively than bison (Singer and Norland 1994), preferentially grazing more nutritious species compared with bison. Thus, these feeding behaviors may have resulted in different grassland plant compositions that responded to herbivory differently. However, we found that study period had no influence on how grazers changed the percentage graminoid biomass in grassland, suggesting that different responses of ANPP to grazing among study periods were not a function of systematic differences in the grass/forb composition in elk- vs. bison-grazed grassland. Thus, the long duration of grazing during the bison-dominant study resulted in grazing intensities exceeding levels that maximized ANPP in YNP.

The finding that the high grazing intensities measured during the bison-dominant study were associated with the right-hand, downward portion of the unimodal stimulation–GI relationship (Fig. 5) is consistent with grassland ANPP increasing when herbivory was experimentally reduced (Fig. 6) at our grassland sites. Although site condition was not included in the best fit model that described stimulation in Fig. 5, we found that stimulation varied substantially between the mesic and dry sites when grazing intensities were manipulated and the response of stimulation over a range of grazing intensities could be directly compared between grasslands. The lower peak level of percentage stimulation occurring at a lower grazing intensity at the dry grassland compared with the mesic grassland may have been a combined function of fewer soil resources available for plants to regrow after being grazed and more stress-tolerant, slower growing plants at the dry compared with the mesic site. These results from the grazing manipulation experiment parallel other studies (Milchunas and Lauenroth 1993, De Mazancourt et al. 1998, Porensky et al. 2013), indicating that grazing intensity and/or site condition can interact to determine ANPP.

This study indicates that a shift in the ungulate grazing community in northern YNP and the feeding behavior of the dominant species have important consequences on grassland ANPP.

Season-long grazing by bison resulted in higher grazing intensities and lower ANPP than when elk dominated the northern ungulate community. High grazing rates by the bison-dominant community did not reduce ANPP below that of ungrazed grassland. However, effects of the large YNP northern bison herd should continue to be monitored to determine whether grazing intensities increase or whether ANPP should be progressively affected by sustained relatively high herbivory rates.

Acknowledgments

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